VOL. 45 JUNE 1918 NO. 6

JUN 24 1918
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BULLETIN

OF THE

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PUBLISHED FOR THE CLUB
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

THE TORREY BOTANICAL CLUB

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PUBLICATIONS

All subscriptions and other business communications relating to the publications of the Club should be addressed to the Treasurer, Dr. Bernard O. Dodge, Dept. of Botany, Columbia University, New York City.

Bulletin. Monthly, established 1870. Price, $4.00 a year; single numbers 40 cents. Of former volumes, only 24–43 can be supplied separately; certain numbers of other volumes are available, but the entire stock of some numbers has been reserved for the completion of sets. Manuscripts intended for publication in the BULLETIN should be addressed to the Editor, Osborn Botanical Laboratory, Yale University, New Haven, Connecticut. Papers should not exceed twenty pages in length, and illustrations (other than zinc etchings) should be limited to one page of half tones or one plate for each ten pages of text. Longer and more copiously illustrated papers, however, may be published if the excess pages and illustrations are paid for by the contributors.

Torreya. Monthly, established 1901. Price, $1.00 a year. Manuscripts intended for publication in TORREYA should be addressed to Norman Taylor, Editor, Brooklyn Botanic Garden, Brooklyn, N. Y.

Memoirs. Occasional, established 1889. (See last pages of cover.)

Preliminary Catalogue of Anthophyta and Pteridophyta within 100 miles of New York City, 1888. Price, $1.00

Reprints. Contributors of articles accepted for publication in the BULLETIN should order reprints, if desired, when they return galley proof to the editor. 25 copies of reprints without cover may be had gratis. If cover is wanted, or if more than 25 copies are wanted, they may be ordered through the editor at the following rates from The New Era Printing Co., Lancaster, Pa., contributor paying for all his reprints.

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200 copies	2.15	3.24	3.92	5.25	6.52	6.92

Covers: 25 for $1.00, additional covers 1¼ cent each.
Plates for reprints, 50 cents each per 100.

Vol. 45 No. 6

BULLETIN

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TORREY BOTANICAL CLUB

JUNE, 1910

A carrier of the mosaic disease

MAKOTO NISHIMURA

(WITH PLATE 7)

INTRODUCTION

The symptoms and general character of the mosaic disease of tobacco and other solanaceous plants are becoming very well known through the work of Mayer (1886), Sturgis (1900), Woods (1899, 1902), Lowe (1900), Iwanowski (1903), Hunger (1905), Clinton (1908), Westerdijk (1910), Peters (1912), Allard (1914, 1915, 1916, 1917), Chapman (1913, 1916), Jensen (1913), and Freiberg (1917).

The disease has been observed on all varieties of *Nicotiana Tabacum*, on several of the more distinct varieties of tomato, on *Petunia violacea*, on *Physalis* (two distinct garden species), on *Datura Stramonium* and *D. Tatula*, on *Hyoscyamus niger*, on *Solanum nigrum* and *S. carolinense* and on several of the more distinct varieties of *Capsicum*. It has been transferred to all these from infected *N. Tabacum*. To this list should be added now *Solanum aculeatissimum*, the apple of Sodom, an infected plant of which was brought from Florida to the greenhouse of Columbia University in the winter of 1915.

According to Allard (1914) the following symptoms are characteristic of different phases of the disease at one or another stage in the infection: (1) partial or complete chlorosis, (2) curling of the leaves, (3) dwarfing and distortion of the leaves, (4) blistered or

[The BULLETIN for May (45: 167–218) was issued May 23, 1918.]

"Savoyed" appearance of the entire plant, (5) mottling of the leaves with different shades of green, (6) dwarfing of the entire plant, (7) dwarfing and distortion of the blossoms, (8) blotched or bleached corollas (in *N. Tabacum* only), (9) mosaic sucker growth, (10) death of tissue (sometimes very marked in *N. rustica*). To these should be added the narrowing of the leaves or frenching and their sometimes uniformly lighter or more yellowish green color.

In attempting to infect the alkekengi or bladder cherry (*Physalis Alkekengi*) I have found that although this plant when inoculated does not show any of the above visible symptoms, it may, nevertheless, become a carrier of the disease in the fullest sense, for I have infected *N. Tabacum* and the apple of Sodom with the juice of plants of the alkekengi which appeared to be entirely free from mosaic.

Allard reports (1914) that he has readily transferred the disease from tobacco to two distinct garden species of *Physalis*, which then showed the general symptoms of the disease, but he does not tell us what species of *Physalis* he used.

As grown by me the alkekengi certainly shows none of the ordinary symptoms, the plants remaining healthy in appearance for indefinite periods, after inoculation with the juice of diseased tobacco or apple of Sodom.

Allard (1917) reports some very interesting experiments on the behavior of the mosaic disease in *N. glauca*. He inoculated this species from diseased plants of *N. Tabacum* and found that the symptoms were confined to a sparse and indistinct mottling along the veins of some of the leaves. This mottling in some instances was too faint to be detected readily, except in transmitted light. Eight of these plants which showed these symptoms more clearly were tested by injecting the expressed sap of each into a series of plants of *N. Tabacum*. The sap of all proved exceptionally virulent, producing in most instances 100 per cent. of infection in each lot of ten plants. After the initial expression of the disease in *N. glauca*, Allard reported that the symptoms gradually became more attenuated, until they were barely distinguishable. In July three of these plants were cut back severely and were immediately transplanted to the field. Growth was resumed, but

no symptoms of the mosaic disease whatever could be detected. However, inoculation tests demonstrated that the sap of these plants contained the infective principle of the disease. These plants were again taken from the field and transplanted into the greenhouse for the winter. Although growth appeared normal and symptoms of the mosaic disease could not be detected with certainty, experiments showed repeatedly that the infective principle of the disease was still present in the expressed sap. Allard further shows that when scions of the immune species, *N. glutinosa*, are grafted upon mosaic-diseased plants of *N. Tabacum* the infective principle of the disease may pass into *N. glutinosa* without the subsequent development of symptoms in it.

These experiments bear an interesting relation to my own observations on the alkekengi as a carrier of the disease. A so-called carrier of the disease is, first, an organism which through acquired toleration continues to harbor the germ or virus after recovery from the diseased condition; or second, one which through natural toleration may acquire and transmit the germ or virus without itself showing any symptoms or suffering in any way from the disease. A third type of carrier is found in those organisms which are immune, but may passively transmit a disease (as does *Abutilon arboreum* in Baur's grafting experiments), without necessarily becoming a seat for the multiplication of the germ or the increase of the virus. See Baur (1906).

MATERIAL AND METHODS

I have used two species of plants as a source of the mosaic disease, namely:

1. Apple of Sodom (*Solanum aculeatissimum*). The first plant of this species showing the mosaic disease was brought from Florida by Professor Harper in December, 1915. So far as I am aware this plant has not hitherto been reported as showing mosaic, though there is of course every reason to suppose that most of the species of *Solanum* are susceptible. The symptoms in apple of Sodom include all those enumerated above.

2. Tobacco (*Nicotiana Tabacum*). I have used the juice of mosaiced plants of the tobacco, kept as stock cultures in the greenhouse of Columbia University.

The juice for inoculation was procured by crushing the leaves. The inoculations were made in several different ways as follows:

No. 1. One stab in each node. In addition to the puncture the four upper leaves were rubbed on both surfaces with the same inoculum used for the needle stab.

No. 2. Five stabs on stem in the following places: one at the tip, one at the base, and three at equal distances between tip and base. Besides these punctures the five upper leaves were rubbed on both surfaces with the same inoculum as used for the stabs.

No. 3. Four stabs: one in the growing tip of stem, and three additional punctures on each in the base of the three upper young leaves near the midrib.

No. 4. Four stabs: one in growing tip of stem, one in middle of stem, a third in its base, and a fourth on the youngest leaf near the midrib.

No. 5. Three stabs on the stem: one in growing tip, one in the middle, and another one near the base of the stem.

No. 6. Four stabs: one in the growing tip of the stem, another in the middle of the stem, the third and fourth on the base of the upper two young leaves near the midrib.

No. 7. One stab in the growing tip of the stem.

No. 8. Two stabs: one in the middle of the stem and another in the blade of the youngest leaf.

EXPERIMENTS

1. *Inoculation of the alkekengi with juice of infected apple of Sodom plants.*

On May 21, forty-eight young plants (3–5 inches high) of the alkekengi were transplanted into five and a half inch pots from the garden and brought into the greenhouse. These were entirely free from mosaic disease and produced fine new growths in two weeks' time.

On June 5, nine plants out of the forty-eight were inoculated with the juice of *S. aculeatissimum* having the mosaic disease. I used method No. 1 in this experiment. No symptoms of the disease appeared in any of these plants. They were entirely indistinguishable from the controls. On June 27 these same nine plants were inoculated again by the same method as before. On

July 16 each plant was examined carefully, but there was no visible evidence of the disease.

On June 25 another series of inoculations with juice of diseased tobacco plants was made on fourteen healthy plants of the alkekengi. These plants were inoculated by method No. 2. After four weeks, although growth continued normally, they showed no symptoms of the disease.

The same experiment was repeated with another series of mature plants of the alkekengi (10–12 inches high). On August 4, twenty of these plants were inoculated with the juice from diseased *S. aculeatissimum*, another series of twenty plants were inoculated with the juice of diseased *N. Tabacum*. Method of inoculation No. 2 was used. After a period of thirty days no symptoms of the disease had appeared on the plants in these two series of experiments. See FIG. 1.

2. *Transfer of mosaic from the apple of Sodom to the alkekengi and then to tobacco*

It occurred to me that the plants might carry the disease, though not showing symptoms, and I inoculated plants of *N. Tabacum* and apple of Sodom with the juice from the alkekengi plants which had been inoculated from the apple of Sodom apparently without results.

TABLE I

SUMMARY OF EXPERIMENT NO. 2

No.	Date of inoculation	First symptom	Incubation period, days	25 days after inoculation
1	July 16	July 23, mosaic on the first new leaf	7	Disease developing
2	" "			No reaction
3	" "	July 24, mosaic on the first new leaf	8	Disease developing
4	" "	July 25, mosaic on the first new leaf	9	" "
5	" "	July 24, mosaic on the first new leaf	8	" "
6	" "			No reaction
7	" "	July 23, mosaic on the first new leaf	7	Disease developing
8	" "	July 24, mosaic on the first new leaf	8	" "
9	" "	July 25, mosaic on the first new leaf	9	" "
10	" "			No reaction
11	" "	July 23, mosaic on the first new leaf	7	Disease developing
12	" "			No reaction
13	" "			" "

On July 16 thirteen young healthy plants of *N. Tabacum* (six- to ten-leaf stage) were inoculated with the juice of the *P.*

Alkekengi which had been inoculated on June 5 and June 27 with the juice of mosaiced leaves of apple of Sodom. In this experiment inoculation method No. 3 was used. July 23, experimental plants 1, 7 and 11 showed mosaic on the first new leaves which were just appearing. July 24, plants 3, 5 and 8 also showed mosaic on the first new leaves. Finally on July 25, plants 4 and 9 exhibited mosaic on the first new leaves and these plants continued diseased, but plants 2, 6, 10, 12 and 13 did not show any symptoms whatever. Eight plants were left as controls and at the end of twenty-five days they showed no symptoms of mosaic. See TABLE I and FIG. 2.

3. *Transfer of mosaic from the tobacco to the alkekengi and then back to the tobacco*

I next tested plants of the alkekengi of the series which had been inoculated with mosaic from diseased tobacco plants with respect to their power to infect tobacco.

July 22, six young healthy tobacco plants (six- to eight-leaf stage) were inoculated with the juice of the alkekengi which showed no symptoms of the disease, although they had been inoculated with the juice of diseased tobacco on June 25. This inoculation was made by method No. 3. July 28, plant 3 showed mosaic on the first new leaf. July 29, plant 1 showed mosaic on the first new leaf. July 30, plants 2 and 5 showed mosaic on the first new leaf, but plants 4 and 6 did not show symptoms of the disease. For this experiment six control plants were kept, which after twenty-five days showed no mosaic.

The experiment was repeated in the period from August 8 to September 2.

August 8, twelve young healthy tobacco plants (six- to ten-leaf stage) were inoculated by method No. 4. August 15, plant 10 showed mosaic on the first new leaf. August 16, plants 7 and 14 showed mosaic on the first new leaves. August 17, plants 9, 11, 15 and 16 showed mosaic on the first new leaves. August 18, plants 12 and 18 showed mosaic on the first new leaves. August 19, plant 17 showed mosaic on the first new leaf.

All of the inoculated plants developed the disease except plants 8 and 13 which did not show any symptoms. In this experiment

twelve plants were kept as controls and after twenty-five days they were found to be free from any symptoms of mosaic. See TABLE II.

TABLE II

SUMMARY OF EXPERIMENT NO. 3

No.	Date of inoculation	First symptoms	Incubation period, days	25 days after inoculation
1	July 22	July 29, mosaic on the first new leaf	7	Disease developing
2	" "	July 30, mosaic on the first new leaf	8	" "
3	" "	July 28, mosaic on the first new leaf	6	" "
4	" "			No reaction
5	" "	July 30, mosaic on the first new leaf	8	Disease developing
6	" "			No reaction
7	Aug. 8	Aug. 16, mosaic on the first new leaf	8	Disease developing
8	" "			No reaction
9	" "	Aug. 17, mosaic on the first new leaf	9	Disease developing
10	" "	Aug. 15, mosaic on the first new leaf	7	" "
11	" "	Aug. 17, mosaic on the first new leaf	9	" "
12	" "	Aug. 18, mosaic on the first new leaf	10	" "
13	" "			No reaction
14	" "	Aug. 16, mosaic on the first new leaf	8	Disease developing
15	" "	Aug. 17, mosaic on the first new leaf	9	" "
16	" "	" " " " " " " " "	9	" "
17	" "	Aug. 19, mosaic on the first new leaf	11	" "
18	" "	Aug. 18, mosaic on the first new leaf	10	" "

4. *Inoculation of the tobacco with juice of healthy alkekengi plants*

To prove that the juice of uninoculated plants of the alkekengi will not produce the disease in tobacco twelve healthy young *N. Tabacum* plants (ten- to eleven-leaf stage) were inoculated on September 10 with the juice of the leaves of healthy *P. Alkekengi* by method No. 3, the same which was used in experiment No. 2. After thirty days two new leaves or more appeared on each plant but did not show any symptoms of the disease.

5. *Comparison of inculation periods*

To compare the length of the incubation period in my transfers through *P. Alkekengi* with the ordinary incubation period when tobacco is inoculated with juice from diseased tobacco, a series of inoculations was made using methods Nos. 4, 7, and 8; twenty plants of *N. Tabacum* were used in each of the three series. The first series were inoculated on March 28 by method No. 8, the plants having eight to ten leaves. The second series were inoculated on April 5 by method No. 7, the plants having five to seven leaves.

The third series were inoculated on August 10 by method No. 4, the plants having seven to eight leaves. Forty-eight of these showed the symptoms of disease. The incubation period was from six to seven days in each of the series. The mosaic symptoms always appeared on the first or second new leaves that were formed after inoculation. Fifteen controls were kept in each experiment and after twenty-five days they were found to be in a healthy condition. The incubation period is seen to be much the same in all the experiments:

In experiment No. 2, from 7 to 9 days;
In experiment No. 3, from 7 to 11 days;
In experiment No. 5, from 6 to 10 days.

This result agrees with the observations of other authors on the length of the incubation period. In each experiment the mosaic was observed on the first or second new leaf which appeared after inoculation.

The appearance of the mosaic leaves of apple of Sodom and tobacco, infected through the alkekengi, is the same in design and coloring (i. e., distribution of the dark green with relation to the vein, etc.) as in direct infection from tobacco to tobacco.

There can be no question that the virus induces the same symptoms after passing through the apparently immune plant as when transferred directly from one susceptible plant to another. The affected plants developed the disease on all new leaves which appeared after inoculation.

6. *Transfer of mosaic from the apple of Sodom to the alkekengi and then back to the apple of Sodom*

The transfer through *P. Alkekengi* from apple of Sodom to apple of Sodom is equally easy.

June 23, ten young healthy plants of apple of Sodom (3–4 inches high) were inoculated with the juice from the leaves of the same plants of *P. Alkekengi* (inoculated from apple of Sodom) which were used in experiment No. 2 as a source for the inoculation of tobacco. I used method No. 5 for this inoculation. June 30, plants 2 and 6 showed mosaic on the first new leaves. July 1, plant 4 showed mosaic on the first new leaf. July 2, plants 7 and

10 showed mosaic on the first new leaves. July 3, plant 1 showed mosaic on the first new leaf. These six plants developed the disease, but plants 3, 5, 8 and 9 showed no symptoms.

On July 20, the same experiment was repeated with another series of ten young healthy plants of apple of Sodom 4–5 inches high. July 29, plant 12 showed mosaic on the first new leaf. July 30, plants 11 and 13 showed mosaic on the first new leaves. July 31, plants 14 and 16 showed mosaic on the first new leaves. August 1, plants 19 and 20 showed mosaic on the second new leaves. Plants 15, 17 and 18 showed no symptoms.

Ten plants were kept in each experiment as controls and after twenty-five days they were found to be in healthy condition.

TABLE III

SUMMARY OF EXPERIMENT NO. 6

No.	Date of inoculation	First symptom	Incubation period, days	25 days after inoculation
1	June 23	July 3, mosaic on the first new leaf	10	Disease developing
2	" "	June 30, mosaic on the first new leaf	7	" "
3	" "			No reaction
4	" "	July 1, mosaic on the first new leaf	8	Disease developing
5	" "			No reaction
6	" "	June 30, mosaic on the first new leaf	7	Disease developing
7	" "	July 2, mosaic on the first new leaf	9	" "
8	" "			No reaction
9	" "			" "
10	" "	July 2, mosaic on the first new leaf	9	Disease developing
11	July 20	July 30, mosaic on the first new leaf	10	" "
12	" "	July 29, mosaic on the first new leaf	9	" "
13	" "	July 30, mosaic on the first new leaf	10	" "
14	" "	July 31, mosaic on the first new leaf	11	" "
15	" "			No reaction
16	" "	July 31, mosaic on the first new leaf	11	Disease developing
17	" "			No reaction
18	" "			" "
19	" "	Aug. 1, mosaic on the second new leaf	12	Disease developing
20	" "	Aug. 1, mosaic on the second new leaf	12	" "

7. *Inoculation of the apple of Sodom with the juice of healthy alkekengi plants*

To prove that the juice of uninoculated plants of *P. Alkekengi* will not produce the disease in the apple of Sodom, twelve healthy young plants of apple of Sodom (5–6 inches high) were inoculated on September 12 with the juice of the leaves of healthy *P. Alke-*

kengi by the method used in experiment No. 6. After a period of four weeks two or three new leaves had appeared on each plant but no symptoms of the disease had appeared.

8. *Transfer of mosaic from the tobacco to the alkekengi and then to the apple of Sodom*

To make the evidence still more clear that *P. Alkekengi* is a carrier, I tried an inoculation of the apple of Sodom with the juice of *P. Alkekengi* used in experiment No. 3, that is from plants inoculated from tobacco. The experiment is the reverse of experiment No. 2.

August 20, twelve young healthy plants of apple of Sodom (4–5 inches high) were inoculated with the juice of the leaves of *P. Alkekengi* which had been inoculated with the juice of mosaic leaves of *N. Tabacum*. Four punctures were made in each plant by method No. 6. August 30, plants 2, 3 and 10 showed mosaic on the first new leaves. August 31, plants 1, 9 and 11 also showed mosaic on the first new leaves. September 1, plant 5 showed mosaic on the second new leaf. September 2, plant 7 showed mosaic on the second new leaf. These eight plants developed the disease, but plants 4, 6, 8 and 12 did not show any symptoms.

TABLE IV

SUMMARY OF EXPERIMENT NO. 8

No.	Date of inoculation	First symptoms	Incubation period, days	25 days after incubation
1	Aug. 20	Aug. 31, mosaic on the first new leaf	11	Disease developing
2	" "	Aug. 30, mosaic on the first new leaf	10	" "
3	" "	" " " " " " " "	10	" "
4	" "			No reaction
5	" "	Sept. 1, mosaic on the second new leaf	12	Disease developing
6	" "			No reaction
7	" "	Sept. 2, mosaic on the second new leaf	13	Disease developing
8	" "			No reaction
9	" "	Aug. 31, mosaic on the first new leaf	11	Disease developing
10	" "	Aug. 30, mosaic on the first new leaf	10	" "
11	" "	Aug. 31, mosaic on the first new leaf	11	" "
12	" "			No reaction

In this experiment twelve controls were kept and after twenty-five days they were found to be in healthy condition. See TABLE IV and FIG. 3.

9. *Inoculation of the apple of Sodom with juice of infected tobacco plants*

Before making the above experiments with the alkekengi I had already satisfied myself as to the relation of the mosaic of tobacco to that of the apple of Sodom.

Forty young healthy plants of apple of Sodom (4–6 inches high) were used in each of the two series. The first series was inoculated on March 27 with juice from diseased apple of Sodom. The second series was inoculated on March 25 with juice from diseased tobacco. These inoculations were made by method No. 5. In the first series thirty-three plants showed mosaic. The incubation period was from eight to ten days. In the second series thirty-six plants showed mosaic. The incubation period was from seven to twelve days. In every case the mosaic symptoms appeared on the first or second new leaves that were formed after inoculation. The incubation period was much the same in all these experiments. Twenty-five controls were kept and after thirty days they were found to be in healthy condition.

The appearance of the mosaic leaves of apple of Sodom, produced by infection from the carrier, *P. Alkekengi* (which had been inoculated from apple of Sodom or from tobacco) is the same as in the case of direct infection from tobacco or apple of Sodom in the distribution of the dark green with relation to the veins, in the blistering, etc. There can be no question that the virus induces the same symptoms after passing through the apparently immune plant to another as when transferred directly from one susceptible to the disease.

10. *Reinoculation of tobacco plants*

The *N. Tabacum* plants inoculated in experiments 2, 3, and 4, which did not take the disease, were later used for further inoculations with virus from the diseased tobacco which had been inoculated from *P. Alkekengi*. September 10 the fourteen plants of *N. Tabacum* were inoculated by method No. 1. September 18, plants 3 and 5 showed the mosaic on the first new leaves. September 19, plants 7 and 11 also showed the mosaic on the first new leaves. September 20, plants 8, 10 and 12 showed the mosaic. September 21, plants 2, 6 and 9 showed the mosaic. September

22, plant 13 showed the mosaic on the second new leaf. These eleven inoculated plants developed the disease, but plants 1, 4 and 14 did not show any symptoms.

It is evident that the failure to infect these plants in the earlier inoculations was due to the uncertainties of the method of inoculation. Twelve of these same plants were kept as controls (four plants which had been used in experiment No. 2, five plants from experiment No. 3 and the other three plants from experiment No. 4). All of the controls but one remained in a healthy condition. The results show that the chances of accidental inoculations in the greenhouse where the work was carried on were very small. These control plants with one exception had remained uninfected for over two months.

11. *Reinoculation of apple of Sodom plants*

The same test was made on the plants of the apple of Sodom which had remained healthy after inoculation in the earlier experiments.

September 13, the twelve plants of apple of Sodom of experiments 6, 8 and 9, which had failed to develope the disease were inoculated by method No. 6 with juice from diseased tobacco which had been inoculated from *P. Alkekengi*. September 21, plants 8 and 11 showed the mosaic on the first new leaves. September 22, plants 7 and 6 showed the mosaic as above. September 23, plants 2, 4 and 5 showed the mosaic as above. September 24, plant 9 showed the mosaic as above. September 25, plant 12 showed the mosaic on the second new leaf.

Nine plants developed the disease, but plants, 1, 3 and 10 did not show any symptoms.

SUMMARY

Physalis Alkekengi is found to be a carrier of the mosaic disease without itself showing any symptoms. The experimental results were as follows:

1. Thirty-four healthy plants of *Physalis Alkekengi* were inoculated with juice of mosaic-diseased plants of *N. Tabacum* and showed no symptoms. To test the method of inoculation and the virulence of the disease sixty young healthy plants of *N.*

Tabacum were inoculated with juice of the mosaic-diseased tobacco and forty-eight of these plants showed the disease.

2. The same test was made with the juice of mosaic-diseased *Solanum aculeatissimum* on twenty-nine healthy plants of *P. Alkekengi*, and none showed any symptoms of the disease. Of forty healthy plants of *S. aculeatissimum* inoculated with juice of mosaic-diseased *S. aculeatissimum* thirty-three plants showed the disease.

3. Of thirty-one healthy plants of *N. Tabacum* inoculated with juice from leaves of *P. Alkekengi* which showed no symptoms of mosaic but had been inoculated from diseased tobacco or *S. aculeatissimum*, twenty-two plants showed typical mosaic disease. Of twelve young healthy plants of *N. Tabacum* inoculated with juice from leaves of *P. Alkekengi* which had not been inoculated none showed the disease.

4. Of thirty-two healthy plants of *S. aculeatissimum* inoculated with juice from leaves of *P. Alkekengi* which showed no symptoms of mosaic but had been inoculated from diseased tobacco or *S. aculeatissimum*, twenty-one plants showed mosaic also. Of twelve young healthy plants of *S. aculeatissimum* inoculated with juice from leaves of *P. Alkekengi* which had not been inoculated, none showed the disease.

5. Experiments have shown that the mosaic diseases of *S. aculeatissimum* and *N. Tabacum* are similar with respect to the symptoms and incubation periods.

6. The juice from diseased *N. Tabacum* when passed through *P. Alkekengi* to *N. Tabacum* has produced the disease in 80 per cent. of the inoculations on healthy plants of *S. aculeatissimum* or *N. Tabacum*. It is evident that there is no marked weakening of the virus by the carrier *P. Alkekengi*.

The author is especially indebted to Professor Harper of Columbia University for his kindly interest and valued supervision throughout these experiments.

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LITERATURE CITED

Allard, H. A. (1914). The mosaic disease of tobacco. U. S. Dept. Agr. Bull. 40: 1–33.

——— (1914). A review of investigations of the mosaic disease of tobacco, together with a bibliography of the more important contributions. Bull. Torrey Club **41**: 435–458.

——— (1915). Distribution of the virus of the mosaic disease in capsules, filaments, anther, and pistils of affected tobacco plants. Jour. Agr. Res. **5**: 251–256. *pl. 33*.

——— (1916). The mosaic disease of tomatoes and petunias. Phytopathology **6**: 328–336.

——— (1917). The mosaic disease of tobacco. Jour. Agr. Res. **10**: 615–631.

Baur, E. (1906). Ueber die infektiose Chlorose der Malvaceen. Sitzungsber. K. Preus. Akad. Wiss. Math.-Naturw. Kl. **32**: 11–29.

Chapman, G. H. (1913). "Mosaic" and allied diseases with especial reference to tobacco and tomatoes. Rept. Mass. Agr. Exp. Sta. **25**: 94–104.

——— (1916). The effect of colored light on the mosaic disease of tobacco. Science II. **44**: 537–538.

Clinton, G. P. (1915). Chlorosis of plants with special reference to calico of tobacco. Conn. Agr. Exp. Sta. Rept. 1914: 537–424. *pl. 25–32*.

Freiberg, G. W. (1917). Studies in the mosaic disease of plants Ann. Missouri Bot. Gard. **4**: 175–232.

Hunger, F. W. T. (1905). Untersuchungen und Betrachtungen über die Mosaik-Krankheit der Tabakspflanze. Zeitschr. Pflanzenkr. **15**: 257–311.

Iwanomski, D. (1903). Ueber die Mosaikkrankheit der Tabakspflanze. *Ibid.* **13**: 2–41.

Jensen, H. (1913). Mosaick-Zcikta. Mededeelingen von "Het proef station voor Vorstenlandsche Tabak" **5**: 61–67.

Lowe, O. (1900). Remarks on the mosaic disease of the tobacco plant. U. S. Dept. Agr. Rept. **65**: 24–27.

Mayer, A. (1886). Ueber die Mosaik krankheit des Tabaks. Landw. Versuchs Stat. **22**: 450–467.

Peters, L. (1912). Krankheiten und Beschädigungen des Tabaks. Mosaikkrankheit Mitteil. Kais. Biol. Anst. Land. Forstrw. **13**: [58].

Sturgis, W. C. (1900). On the effects on tobacco of shading and application of lime. Conn. Agr. Exp. Sta. Rept. **23**: 259–261.

Westerdijk, J. (1910). Die Mosaikkrankheit der Tomaten. Phytopath. Lab. "Willie Commelin Scholten," Mededeel. **1**: 1–20.

Woods, A. F. (1899). The destruction of chlorophyll by oxidizing enzyms. Centralbl. Bakt. Abth. II. **5**: 745–754.

——— (1902). Observations on the mosaic disease of tobacco. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 18: 1–24. *pl. 1–6.*

Explanation of plate 7

FIG. 1. Typical leaf of *Physalis Alkekengi*, the carrier of the mosaic disease, inoculated with the juice of the leaves of *Solanum aculeatissimum* having mosaic disease but not showing any symptoms of the disease.

FIG. 2. Typical mosaic leaf of *Nicotiana Tabacum*, inoculated with the juice of the leaves of *Physalis Alkekengi* which had been inoculated with the juice of mosaic leaves of *Solanum aculeatissimum*.

FIG. 3. Typical mosaic leaf of *Solanum aculeatissimum*, inoculated with the juice of *Physalis Alkekengi* which had been inoculated with the juice of mosaic leaves of *Nicotiana Tabacum*.

The air chambers of Grimaldia fragrans*

ALEXANDER W. EVANS

(WITH FOURTEEN TEXT FIGURES)

INTRODUCTION

In most of the Marchantiales the thallus shows a layer of green tissue with air spaces or chambers below the dorsal epidermis. These chambers exhibit many differences when the group as a whole is considered, but it is possible to refer the majority to three distinct types. To these the names of the representative genera *Riccia*, *Reboulia* and *Marchantia* may be applied.

In the *Riccia* type the chambers occupy a single layer and are in the form of canals with their long axes approximately vertical; the canals are usually narrow and bounded by only four rows of cells, but in certain cases they are broader and bounded by a greater number of cells. In the *Reboulia* type the chambers are in two or more layers (at least in the median portion of the thallus) and are in the form of irregular polyhedrons, often tending to be isodiametric; this type is sometimes complicated by cellular outgrowths into the chambers. In the *Marchantia* type the chambers are again in a single layer (as in the *Riccia* type) but are in the form of more or less flattened polygonal prisms with their longer dimensions approximately horizontal; they are further distinguished by the presence of numerous simple or branched green filaments, extending from the floors of the chambers nearly or quite to the epidermis. In all three types the chambers communicate with the outside air by means of openings in the epidermis. In the *Riccia* type these may be nothing more than continuations of the canalicular chambers, but in the two other types the openings are usually surrounded by specialized epidermal cells and form the characteristic air pores or epidermal pores of the group.

Among North American genera the *Riccia* type is restricted to *Riccia* and *Oxymitra;* the *Reboulia* type is found in *Ricciella*,

* Contribution from the Osborn Botanical Laboratory.

Ricciocarpus, Peltolepis, Sauteria, Clevea, Plagiochasma, Reboulia, Grimaldia, Neesiella, Cryptomitrium, Asterella and *Bucegia;* while the *Marchantia* type occurs in *Corsinia, Targionia, Conocephalum, Lunularia, Preissia* and *Marchantia.* The reduced air chambers of *Cyathodium* conform best perhaps to the *Marchantia* type, in spite of the absence of green filaments, while the adult thallus of *Dumortiera* lacks air chambers altogether.

The genus *Grimaldia* Raddi, as understood by most recent writers, contains about half a dozen species. The most widely distributed of these is *G. fragrans* (Balb.) Corda, which is found in Europe, Asia and North America. Other well-known species, closely related to *G. fragrans,* are the Mediterranean *G. dichotoma* Raddi and the Californian *G. californica* Gottsche. In the eastern parts of the United States *G. fragrans* is sometimes locally abundant, preferring sunny trap ridges and growing on earth among rocks, rather than on the rocks themselves. It was in such a locality as this, on West Rock Ridge, near New Haven, Connecticut, that the material used in the present study was collected. The narrow thallus is firm and compact and produces an abundance of purple ventral scales with bleached-out appendages. The upper surface is grayish green and shows no indications of the boundaries of the air chambers beneath the epidermis. The margins, as well as the ventral surface, are more or less pigmented with purple. The species is markedly xerophytic, the margins becoming involute when dry, thus covering over and protecting the upper surface.

THE AIR CHAMBERS OF THE MATURE THALLUS

The green tissue of the thallus in *Grimaldia* has been repeatedly described, most of the observations having been based on either *G. fragrans* or *G. dichotoma.* Unfortunately the descriptions show marked discrepancies. Stephani (**11**), for example, states that the air chambers are densely filled with erect green filaments composed of long cylindrical cells, and K. Müller (**6**, p. 259) notes the presence of vertical plates of cells in addition to the filaments. Schiffner (**9**, p. 309) criticizes these descriptions. According to his account the chambers of *Grimaldia* undergo a secondary partitioning by means of irregular green lamellae which

grow upward from the floors and lateral walls of the chambers. A spongy tissue is thus formed in which narrow air spaces run, scarcely broader than the thickness of the lamellae, and the original partitions of the chambers soon become unrecognizable. He admits that in section the plates of cells one cell thick look like filaments and that marginal cells of the plates sometimes project as teeth, but he maintains that actual filaments are never present and that this fact is at once made evident by sections of the green tissue cut parallel with the surface of the thallus. Massalongo (5, p. 730), on the other hand, agrees with Stephani and states that the chambers are filled with vertical uniseriate filaments, some of

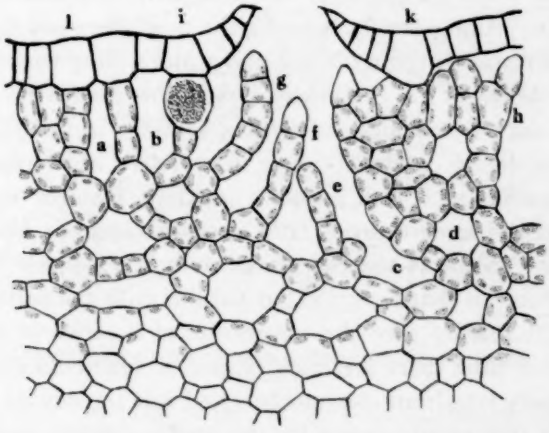

FIG. 1. Transverse section through epidermis and green tissue, × 270. *a–d*, air chambers; *e–g*, apparent filaments; *h*, plate-like outgrowth; *i*, *k*, *l*, boundaries between chambers.

them reaching the epidermis. His figures not only show filaments clearly but indicate that the boundaries of the chambers are distinct, in this respect also differing from Schiffner's account.

The green tissue of *G. fragrans* is so compact that it is difficult to make out its true structure from ordinary hand sections. Even microtome sections are not always easy to interpret, but they give a much clearer idea of the complex arrangement of the cells and of the intricate system of aërating chambers and help to explain some of the conflicting statements in the published descriptions. In a transverse section, such as the one shown in FIG. 1, the cham-

bers are seen to be in three or four layers in the thickened median portion of the thallus. As the margins are approached the thallus becomes thinner, and the number of layers decreases until only the uppermost layer is left. Except in this uppermost layer the chambers are usually polygonal in outline and tend to be isodiametric. In the uppermost layer they tend to be elongated vertically, as shown in the spaces *a* and *b*. That the spaces communicate with one another is also indicated in the figure. The space *c*, for example, is connected with a space nearer the epidermis, and the space *d* probably represents a passageway to a chamber in another section. The figure seems, at first sight, to confirm the statements made by Müller, that both filaments and cell plates are present. Immediately beneath the pore there are apparently three filamentous outgrowths, *e*, *f*, and *g*, and a plate-like outgrowth is clearly shown at *h*. Of course, as Schiffner intimates, apparent filaments may be nothing more than sections of cell plates. In the section drawn careful focusing does indeed show that *e* and *f* are in close contact with another apparent filament in another plane, and the same thing is true of other apparent filaments in the section. Some of the cell plates, moreover, appear to have a fluted surface, so that a section cut parallel with the surface of the plate might readily give the impression of a series of filaments. At the same time there are many apparent filaments which seem to be entirely free from one another, and it is impossible to determine their true status except by the study of other sections. It will be noted that the more deeply situated chambers are free or nearly so from outgrowths of any kind.

The figure is of further interest in showing that some of the apparent filaments and plate-like outgrowths end freely in the chamber without reaching the epidermis, this being especially true in the vicinity of the pores; others, as shown by the one between the spaces *a* and *b*, extend to the very epidermis and seem to be connected with it. It is doubtful, however, if the connection is ever anything more than a close contact, such as the free filaments in *Marchantia* and *Conocephalum* often exhibit. No instance has been observed where an outgrowth extends downward from the epidermis and ends freely in a chamber, and there is no adequate evidence that the epidermal cells themselves ever give

rise to outgrowths, as Schiffner suggests may be the case. The original boundaries of the dorsal air chambers are not absolutely unrecognizable, but they are by no means as distinct as Massalongo's figure represents them. In FIG. 1 the boundaries of the chamber with the air-pore are shown at *i* and *k*, while another boundary is situated at *l*.

The longitudinal section drawn (FIG. 2) brings out the fact that many of the air chambers are more or less elongated. This is strikingly true of those most deeply situated but is also well

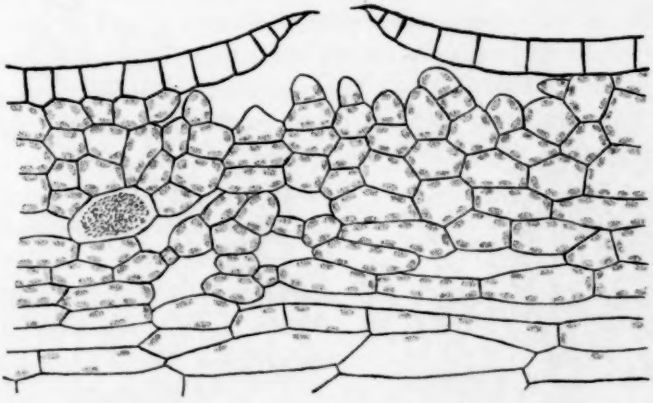

FIG. 2. Longitudinal section through epidermis and green tissue, × 270.

shown by the chamber with the air-pore, although the actual boundaries of this chamber are not definitely indicated. It will be noted that the upper margin of the cell plate represented, which extends almost longitudinally beneath the pore, is distinctly dentate, some of the teeth being over a cell in length. This accords, on the whole, with Schiffner's statement that the marginal cells of the plates may project as teeth. Although some of the teeth shown are more than projecting cells, it would be a stretch of the term to describe them as filaments. The figure, therefore, presents no evidence of the occurrence of true filaments. Other sections, however, show apparent filaments, similar to those represented in FIG. 1.

According to Schiffner, a section through the green tissue parallel with the surface of the thallus will at once show that the chambers are destitute of free filaments. FIG. 3 shows a part of such a

section, cut immediately below the epidermis, and seems at first to belie his statement. The figure shows the partitions, almost complete, of an air chamber, the cells being distinguished by stippling. Only one end of the chamber is represented; the other end did not show because the section was slightly oblique in that region and passed through the epidermis instead of the green tissue beneath. That the stippled cells represent the boundaries of a chamber is evident from their close union and also from the

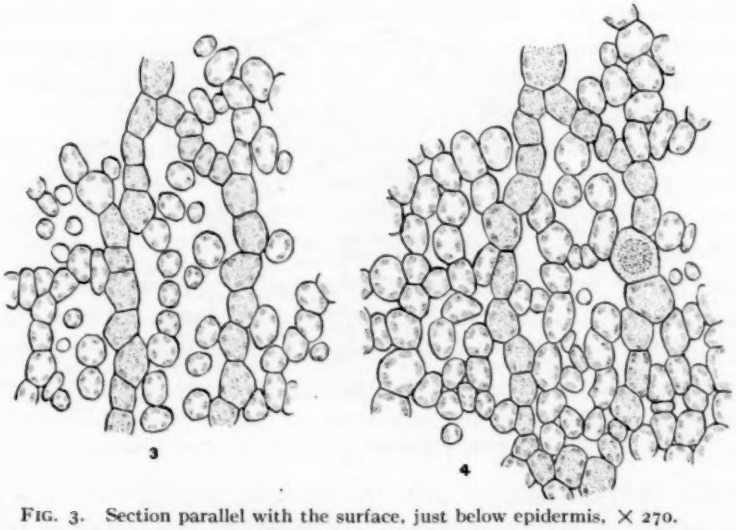

FIG. 3. Section parallel with the surface, just below epidermis, × 270.
FIG. 4. Section a short distance below the one shown in FIG. 3, × 270.

fact that an epidermal pore was situated above the middle of the space which they enclose. It will be seen that the chamber contains a number of cells, circular in section and either entirely free or else loosely connected with one another or with the cells of the partitions. Similar cells are shown elsewhere in the figure, and a superficial examination would interpret them as the sections of filaments, especially if they were considered in connection with FIG. 1.

The incorrectness of this interpretation is brought out by a comparison with FIG. 4, which shows the same chamber at a lower level, the cells of the partitions being again indicated by stippling. In this figure the complete boundaries of the chamber

are shown, but the cells enclosed present a very different appearance. They are not only much more numerous but are, with a few exceptions, more or less firmly united, and the entire chamber is thus divided up into smaller chambers, some of which seem entirely cut off while others show their connections with other chambers. The seven cells shown on the right of the left-hand partition in FIG. 3 are represented in FIG. 4 by seven united cells, showing at once that these seven cells are not the cross sections of filaments but simply the cross sections of teeth, like those shown in FIG. 2. Similar conclusions would be created by comparing other apparently free cells in FIG. 3 with their representatives in FIG. 4. It thus becomes established that there are no free filaments in the chambers. It will be noted further that FIG. 4 presents a much more complicated condition than FIG. 3 and that the boundaries of the air chamber would be hardly distinguishable except through comparison with the simpler figure. It is probable that a section like the one shown in FIG. 4 was responsible for Schiffner's statements, which it certainly strongly supports.

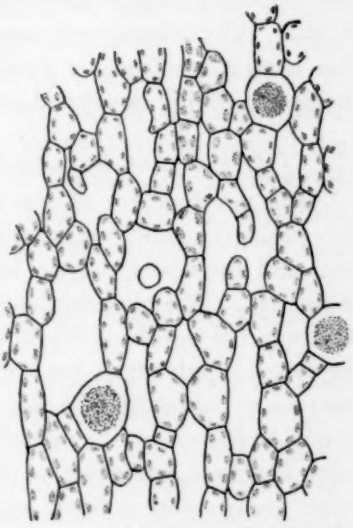

FIG. 5. Section parallel with the surface below the dorsal layer of chambers, × 270.

In FIG. 5 a section from another thallus is shown, cut at a still lower level. This section shows a loose spongy tissue, two of the chambers being connected by a passageway. Cellular outgrowths are very infrequent, but a single cell, apparently free, is shown in one of the chambers, and a single short outgrowth in another. When compared with FIG. 4 the spaces are relatively larger and fewer and the tissue in consequence much less compact. Sections cut farther down show elongated spaces, similar to those represented in FIG. 2, while sections beneath these show the ventral parenchymatous tissue without spaces of any sort.

It is clear from a comparison of transverse, longitudinal and horizontal sections that a distinction may be made between the dorsal layer of air chambers in *Grimaldia* and the more deeply situated layers. In the dorsal layer the original chambers show a secondary partitioning by a system of more or less vertical cell plates, the free margins of which sometimes bear scattered teeth, apparently always less than two cells long. Except for these teeth the chambers lack filaments completely. In the more deeply situated layers, the chambers are much simpler and rarely show evidences of any kind of outgrowth. These conclusions show the incorrectness of certain statements made by Stephani, K. Müller, and Massalongo and the essential correctness of Schiffner's account.

The complex conditions found in the green tissue of *Grimaldia* are duplicated by *Plagiochasma* and by certain species of *Asterella*. The other genera showing the *Reboulia* type of air chamber have a much looser green tissue, the secondary partitioning being less highly developed or absent altogether.

ORIGIN AND ENLARGEMENT OF THE AIR CHAMBERS

The development of the air chambers in the Marchantiales has aroused a good deal of interest among students of the Hepaticae, and the history of the subject is fully given by Barnes and Land (1). The explanation which they advance to account for the origin of the chambers differs in certain respects from the older explanation advanced by Leitgeb and accepted by many of his successors. Leitgeb's explanation was based primarily on his study of *Riccia*, but he extended its application to the more complex genera. According to his ideas the air chambers do not originate in compact tissue, and no splitting of cell walls is involved in their formation. They arise, rather, on the surface of a young thallus and are due to a cessation of upward growth in certain limited areas, the surrounding parts growing upward vigorously. The areas where growth is supposed to cease are situated in most cases where four of the surface cells come together; they mark the lower ends of the chambers, the vertical extent of which depends upon the degree of upward growth which the surrounding parts exhibit.

According to Barnes and Land there is nothing to support Leitgeb's views. In their opinion the chambers always originate in compact tissue below the surface of the young thallus by a splitting of cell-walls and, in case the mature chamber has an epidermal pore, the splitting extends upward until the surface is reached. They based their conclusions on a study of *Ricciella* (*Riccia fluitans* L.), *Ricciocarpus* (*Riccia natans* L.), *Marchantia*, *Lunularia*, *Conocephalum*, *Dumortiera*, *Asterella* (*Fimbriaria*), and *Plagiochasma*, and assumed that they would apply as well to *Riccia* (in its restricted sense). After the chambers are once established their increase in size need not involve any further schizogenous processes. It is largely brought about by the growth of the cells surrounding the chamber, and may be wholly brought about in this way; in other words, by the surface extension of the bounding cell-walls. According to Leitgeb's ideas the increase in the size of the chambers is brought about in much the same way, except that a total absence of splitting is always assumed. It will be seen, therefore, that the most important differences between the two explanations are concerned with the very beginning of the developmental process: according to Leitgeb the chamber is superficial in origin and no splitting occurs; according to Barnes and Land the chamber is not superficial in origin and splitting does occur.

Among recent papers dealing with air chambers, those by Miss Hirsh (**4**), Pietsch (**8**), Deutsch (**3**), Miss O'Keeffe (**7**) and Miss Black (**2**) may be briefly noted. Miss Hirsh's work is based largely on *Ricciocarpus natans* (L.) Corda and *Riccia Frostii* Aust. She reaches the conclusion that the first of these species agrees with Barnes and Land's explanation, while the second agrees with Leitgeb's. Her figures of *R. Frostii*, however, by no means support this conclusion fully. Although they show that the chambers drawn may have been superficial in origin, they show as well that a splitting must sometimes have occurred, because some of the chambers extend below the original surface of the thallus. This is brought out clearly by her *f. 6*, upon which she lays especial emphasis. This figure, in fact, presents no convincing evidence that the chamber may not have been initiated by a schizogenous process.

Pietsch's work is remarkable for its thoroughness and accuracy. It deals with species of *Riccia* and *Ricciella*, and his account is therefore based on the group of plants from which Leitgeb drew his conclusions. Although he criticises the work done by Barnes and Land, his observations lead to similar conclusions, so far as the development of the air chambers is concerned. He finds that even in *Riccia* the chambers originate from a splitting of cell walls, the split beginning below the surface and then extending upward until the surface is reached.

Deutsch's paper, devoted to *Targionia hypophylla* L., includes an interesting observation on the development of the air chambers. He states that they arise by a splitting apart of cells close to the apical cell but maintains that the split begins on the outside and extends inward, instead of beginning below the surface and extending outward. The *f. 3*, which he cites as evidence, would be more convincing if the youngest chamber shown did not extend into the hypodermal tissues; as the figure stands it might equally well bear the opposite interpretation from the one drawn. Deutsch does not consider that his account differs in any essential respect from the explanation of Barnes and Land, in spite of the superficial origin which he assigns to the chambers. Miss O'Keeffe, who also worked on *Targionia*, fully supports Deutsch in his statements about the origin of the chambers. Fortunately, the youngest chamber which she shows (*f. 1, A, a*) seems to be conclusive; it appears in longitudinal section as a split between two superficial cells and does not extend beyond them.

Miss Black's paper deals with *Riccia Frostii*, one of the species investigated by Miss Hirsh, and the same conclusions are drawn as to the origin of the air chambers. Her *f. 6*, however, is open to the same criticism as Miss Hirsh's figures. It represents the apical region of a thallus cut longitudinally and including five young air chambers, but even the youngest of these projects below the original surface, showing that a splitting of a cell wall must have taken place. Miss Black emphasizes the fact that she observed no cases in which an intercellular space appeared below the surface and then broke through to the outside, so that her conclusion regarding the superficial origin of the chambers seems justified. At the same time her figure presents no evidence that

the chambers may not have originated from splits between superficial cells, as Deutsch and Miss O'Keeffe maintain is the case in *Targionia*.

The thallus of *Grimaldia fragrans* is so complex that it is impracticable to trace the cell divisions which take place in the segments cut off from the apical cell, as Pietsch has so ably done in the case of *Riccia glauca* L. FIGS. 6–8, however, give some idea of the apical region and bring out the fact that a single apical cell with four cutting faces is present. In FIG. 6, immediately above the apical cell the meristematic tissue forms a compact mass

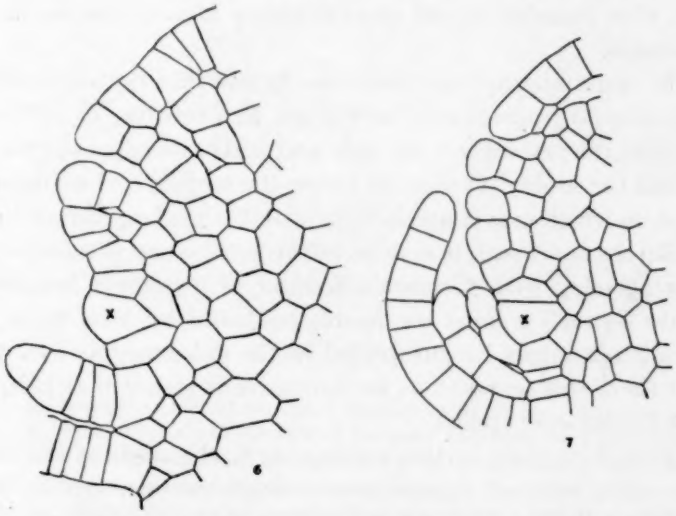

FIG. 6. Longitudinal section through a growing point, × 500. *x*, apical cell.
FIG. 7. Longitudinal section through another growing point, × 500. *x*, apical cell.

without intercellular spaces. Between the fourth and fifth cells the first indication of a chamber appears in the form of a split a short distance below the surface. Between the fifth and sixth cells an older and longer chamber is visible, which has reached the surface, apparently through the upward extension of a similar split. The elongation and widening of the chamber have been largely due, it would appear, to the growth of the bounding cells. The still older chambers shown in the figure are not cut squarely in the middle and need not be further considered.

In FIG. 7, which represents the apical region of another thallus, a somewhat different condition is revealed. In this case the first indication of an air chamber appears between the third and fourth cells and is likewise in the form of a split, but this time the split evidently began on the outside and extended inward. Although the chamber is thus superficial in origin, there is no evidence that a surface area has had its upward growth arrested, as Leitgeb's explanation demands. The split clearly extends inward from the original surface. The chamber between the fourth and fifth cells is considerably deeper and broader, and it is clear that its increase in size has involved further schizogenous processes. The next chamber shown gives evidence of a further horizontal extension.

It would appear from these two figures that the air chambers in *Grimaldia fragrans* owe their origin to a splitting of cell walls, but that the place where the split first makes its appearance is not always the same. It may be below the surface and extend outward, in which case it agrees fully with the explanation advanced by Barnes and Land; it may be at the surface and extend inward, thus agreeing with Deutsch's account of *Targionia hypophylla*. In the writer's opinion the figures published by Miss Hirsh and Miss Black might be interpreted in the same way as FIG. 7, so that there still seems to be no conclusive evidence that Leitgeb's explanation ever applies.

FIGS. 8–10 yield further evidence as to the origin of the chambers; they were all drawn from a single section, cut at right angles to the long axis of the thallus, and show for the most part superficial cells. In FIG. 8 the apical cell appears in the form of a rectangle. Directly above it an air chamber reaching the surface is shown between the fourth and fifth cells, corresponding apparently with the chamber between the fourth and fifth cells of FIG. 7. The schizogenous origin of this chamber seems clear, but there is nothing to show whether the split began at or below the surface. Between the third and fourth cells no signs of a chamber can be discerned, although a superficial split may be present like the one shown in FIG. 7. The figure at any rate gives no evidence of a split beginning below the surface.

FIGS. 9 and 10 are much more conclusive. They represent a

portion of the thallus to the right of the apical cell and derived from lateral segments. In drawing FIG. 9 the microscope was focused on the surface of the cells in a circumscribed area; in drawing FIG. 10 it was focused a little below the surface of the same area. FIG. 9 shows a series of cells in close union and two air chambers which have reached the surface; FIG. 10 shows the same two chambers and six additional ones. The latter clearly represent schizogenous spaces below the surface and demonstrate an origin like that of the youngest chamber in FIG. 6.

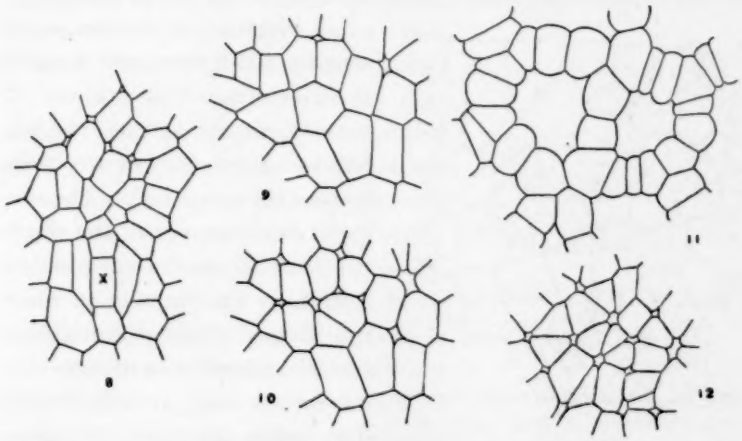

FIG. 8. Transverse section through a growing point, × 500. *x*, apical cell.

FIG. 9. Superficial cells to the right of the apical cell shown in FIG. 8, × 500.

FIG. 10. The same region as that shown in FIG. 9, but at a slightly lower focus, more very young dorsal chambers being visible, × 500.

FIG. 11. Slightly older dorsal chambers than those shown in FIG. 10, the section parallel with the surface, × 500.

FIG. 12. Section just below the one shown in FIG. 11, the numerous intercellular spaces being the beginnings of more deeply situated chambers, × 500.

The rudimentary chambers shown in FIGS. 6–10 represent the beginnings of the complex dorsal chambers shown in FIGS. 1–4. The later stages in the development of these chambers and the origin and development of the more deeply situated chambers are exceedingly difficult to follow. For a while the dorsal chambers are distinct enough in sections cut immediately below the epidermis. Such a section is shown in FIG. 11, where two complete chambers and parts of six others are represented. The increase

in size which these chambers show, when compared with the small intercellular spaces in FIG. 10, is due to the vigorous growth of the bounding cells, accompanied by rapid cell divisions. At this stage the partitions show no evidence of outgrowths. FIG. 12 represents the section just below the one shown in FIG. 11, the cells drawn, in part at least, forming the floors of the dorsal chambers. The figure shows many intercellular spaces, which are clearly schizogenous in origin; these spaces represent the beginnings of the more deeply situated chambers or, in some cases, the passageways leading from these chambers to the dorsal chambers.

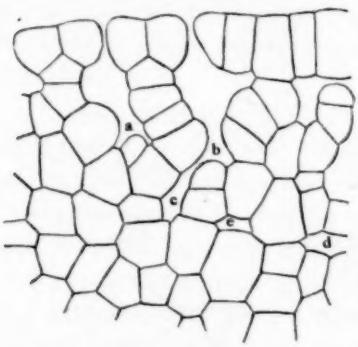

FIG. 13. Longitudinal section through young chambers. × 500. *a–e*, more deeply situated chambers.

A longitudinal section, representing about the same stages as those shown in FIGS. 11 and 12, may be seen in FIG. 13, the left-hand side of the figure being toward the apical cell. The very rapid development of the chambers is clearly indicated, and light is thrown on the way in which the deeper chambers originate, such chambers being indicated by the letters *a–e*. It will be seen that some of these chambers seem to be completely enclosed, showing that they may have originated by a splitting of cell walls in compact tissue, and that others already communicate with more dorsally situated chambers. Whether the connecting passageways are always formed subsequently to the chambers, or whether the formation of the passageways may sometimes precede that of the chambers is not altogether clear. If the older, right-hand side of the figure is compared with the younger, left-hand side, it becomes evident that the tissue with intercellular spaces has almost tripled in thickness and that the dorsal chambers have become distinctly deeper. The rapid growth involved in these changes has taken place in the original partitions of the dorsal chambers, in the cells which formed their irregular floors and in the cells immediately beneath. As the writer conceives the process, the growth of the partitions is both horizontal and

vertical, the growth in the latter direction being often equalled by the upward growth (accompanied by cell division) of the cells forming the floors of the chambers; these in turn remain more or less united with one another and with the cells of the partitions and in this way form the system of united cell-plates in the dorsal chambers. At a later stage the margins of some of the plates which end freely in the chambers give rise to teeth as shown in FIG. 2.

It is difficult to secure direct evidence from the vegetative thallus that the partitions form surface-outgrowths. FIG. 14, however, which is drawn from a section of the young female receptacle, shows that such outgrowths are possible. The section was cut parallel with the upper surface of the receptacle, and the figure shows two complete chambers and parts of eight others; two of the latter contain sections of the tubular epidermal pores which hang down from the roofs of the chambers. The partitions are one cell thick but give the impression of being thicker when cut obliquely. The outgrowths originate as projections of cells which become cut off by walls and then continue their growth and cell-divisions. In the vegetative thallus such outgrowths evidently play a very minor part in the development of the green tissue.

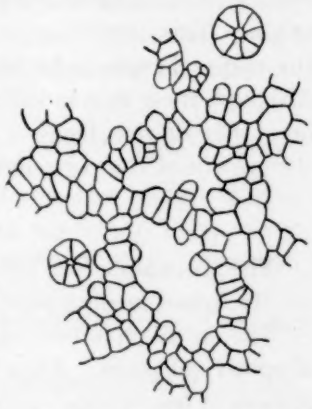

FIG. 14. Section parallel with the surface of a young female receptacle, just below the epidermis, × 270.

The chambers below the dorsal layer make their appearance very early, as seen in FIGS. 12 and 13, although they always appear later than the dorsal chambers. As the thallus becomes differentiated, these chambers increase rapidly in size through the growth of the bounding cells, but the appearance of new chambers, except in the apical region, has not been demonstrated and seems improbable. If schizogenous processes play a part in the enlargement of these chambers, it is only to a very limited extent.

The green tissue in the thallus of *Plagiochasma* bears a strong

resemblance to that of *Grimaldia*. Its development has been described by Miss Starr (10), her investigation having been based on an undetermined species from Mexico. She confirms the earlier observation of Barnes and Land that the air chambers of *Plagiochasma* owe their origin to a splitting of cell walls below the surface. She notes further that the chambers are at first deep and narrow but that they soon become wide and irregular, and she ascribes the changes in size and form which they show to a "stretching and tearing of tissues between neighboring chambers." In other words she considers that schizogenous processes play a leading part in the enlargement of the chambers as well as in their origin. This conclusion is hardly supported by her *f. 11* or by the earlier figures published by Barnes and Land (1, *f. 17–22*). Although these figures indicate a schizogenous origin of the chambers, they do not disprove that the enlargement is mainly due to the growth of the surrounding cells.

SUMMARY

The air chambers of *Grimaldia fragrans* are in several layers in the thickened median portion of the thallus.

The dorsal chambers communicate with the outside by means of epidermal pores. They are subdivided by an irregular system of more or less vertical, united cell plates, enclosing narrow spaces, so that the boundaries of the chambers are difficult to distinguish. The cell plates sometimes reach the epidermis and sometimes do not; in the latter case the free margins sometimes bear scattered teeth, less than two cells in length, especially in the vicinity of the pores. Except for these teeth the chambers lack filaments completely.

The more deeply situated chambers communicate with one another and with the dorsal chambers by means of passageways; they are scarcely or not at all subdivided by cell plates.

The chambers all owe their origin to a splitting of cell walls in closely united tissue. In the case of the dorsal chambers the split sometimes begins below the surface and extends outward; sometimes at the surface and extends inward.

The dorsal chambers appear first, very close to the apical cell, but the more deeply situated chambers appear soon afterwards.

The increase in the size of the chambers is due largely to the growth of the bounding cells and only slightly to further splittings of cell walls. The system of united cell plates in the dorsal chambers and the partitions between the chambers increase in vertical height simultaneously. Direct outgrowths from the surfaces of cell plates play a very small part in the process of subdivision.

The material upon which this investigation was based was collected and prepared by Mr. John F. Logan, who expected to utilize it in his own studies. Through the pressure of other work his plans could not be realized, and his preparations were placed at the disposal of the writer for examination. The writer would therefore express his sincere thanks to Mr. Logan for his courtesy.

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LITERATURE CITED

1. **Barnes, C. R., & Land, W. J. G.** Bryological papers. I. The origin of air chambers. Bot. Gaz. **44**: 197–213. *f. 1–22.* 1907.
2. **Black, C. A.** The morphology of *Riccia Frostii*, Aust. Ann. Bot. **27**: 511–532. *pl. 37, 38.* 1913.
3. **Deutsch, H.** A study of *Targionia hypophylla*. Bot. Gaz. **53**: 492–503. *f. 1–13.* 1912.
4. **Hirsh, P.** The development of the air chambers in the Ricciaceae. Bull. Torrey Club **37**: 73–77. *f. 1–6.* 1910.
5. **Massalongo, C.** Le "Marchantiaceae" della Flora Europea. Atti R. Ist. Veneto **75**: 669–816. *pl. 1–27.* 1916.
6. **Müller, K.** Die Lebermoose Deutschlands, Oesterreichs u. d. Schweiz. In L. Rabenhorst, Kryptogamen-Flora, ed. 2, **6**. Leipzig. 1906–11.
7. **O'Keeffe, L.** Structure and development of *Targionia hypophylla*. New Phytol. **14**: 105–116. *f. 1, 2.* 1915.
8. **Pietsch, W.** Entwicklungsgeschichte der vegetativen Thallus, insbesondere der Luftkammern der Riccien. Flora **103**: 347–384. *f. 1–21.* 1911.
9. **Schiffner, V.** Morphologische und biologische Untersuchungen über die Gattungen *Grimaldia* und *Neesiella*. Hedwigia **47**: 306–320. *pl. 8.* 1908.
10. **Starr, A. M.** A Mexican *Aytonia*. Bot. Gaz. **61**: 48–58. *pl. 1–4* + *f. 30–33.* 1916.
11. **Stephani, F.** *Grimaldia* Raddi. [In Species Hepaticarum **1**: 89–93.] Bull. Herb. Boissier **6**: 792–796. 1898.

INDEX TO AMERICAN BOTANICAL LITERATURE

1911-1918

The aim of this index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

Andrews, E. F. A botanist's suggestion for a national flower. Am. Bot. **24**: 8–10. F 1918.

Andrews, F. M. *Closterium moniliferum.* Proc. Indiana Acad. Sci. **1916**: 323, 324. 1917.

Anthony, R. D. Inheritance of sex in strawberries. New York Agr. Exp. Sta. Tech. Bull. 63: 3–10. S 1917.

Atkinson, G. F. Selected cycles in *Gymnoconia peckiana.* Am. Jour. Bot. **5**: 79–83. 9 Mr 1918.

Beardslee, H. C. The russulas of North Carolina. Jour. Elisha Mitchell Sci. Soc. **33**: 147–198. *pl. 70–111.* Ja 1918.

Blake, S. F. Further new or noteworthy Compositae. Contr. Gray Herb. II. **53**: 23–30. *pl. 1.* 26 F 1918.

Includes ***Cirsium acanthodontum, Liabum hypochlorum, Verbesina Arthurii, Diplostephium denticulatum*** and ***Aphanostephus Kidderi,*** spp. nov.

Blake, S. F. *Lycopodium sabinaefolium* Willd. var. *sharonense* (Blake) comb. nov. Rhodora **20**: 60. 2 Mr 1918.

Blake, S. F. New plants from Oaxaca. Contr. Gray Herb. II. **53**: 55–65. 26 F 1918.

Includes the new genus ***Schismocarpus*** and thirteen new species in various genera.

Blake, S. F. New Spermatophytes collected in Venezuela and Curaçao by Messrs. Curran and Haman. Contr. Gray Herb. II. **53**: 30–55. 26 F 1918.

Includes the new genera *Hecatostemon* and *Oxycarpha*, and 24 new species in various genera.

Burlingham, G. S. New species of *Russula* from Massachusetts. Mycologia **10**: 93–96. Mr 1918.

Four new species are described.

Britton, N. L. An undescribed *Scirpus* from California. Torreya **18**: 36. *f. 1.* 8 Mr 1918.

Scirpus Congdoni sp. nov.

Buchanan, R. E. The evolution of the bacteria. Science II. **47**: 320–324. 29 Mr 1918.

A review of Dr. I. J. Kligler's paper on the evolution and relationship of bacteria containing additional information.

Burkholder, W. H. The anthracnose disease of the raspberry and related plants. Cornell Agr. Exp. Sta. Bull. 395: 155–183. *f. 12–21.* N 1917.

Bush, B. F. The genus *Euthamia* in Missouri. Am. Mid. Nat. **5**: 157–177. Mr 1918.

Carpenter, C. W. Wilt diseases of okra and the *Verticillium*-wilt problem. Jour. Agr. Research **12**: 529–546. *pl. A, 17–27.* 4 Mr 1918.

Clute, W. N. Note and comment. Am. Bot. **24**: 26–33. F 1918.

Includes notes on: Origin of coal, Sir Walter Raleigh's potatoes, The bluet in cultivation, The first frost, *Erigenia bulbosa*, *Lycopsida* and *Pteropsida*, Evolution of the larch, Thymol.

Conard, H. S. Prairie plants for the garden. Jour. Internat. Gard. Club **2**: 129–140. Mr 1918. [Illust.]

Cooper, J. R. Methods of controlling blister canker. Nebraska Agr. Exp. Sta. Bull. 161: 1–18. *pl. 1–7.* 15 D 1917.

Coulter, J. M. A century of botany in Indiana. Proc. Indiana Acad. Sci. **1916**: 236–260. 1917.

Crozier, W. J. Cell penetration by acids—IV. Note on the penetration of phosphoric acid. Jour. Biol. Chem. 33: 463–470. *f. 1–3.* Mr 1918.

Deam, C. C. Plants new or rare to Indiana—VII. Proc. Indiana Acad. Sci. **1916**: 315–322. 1917.

Downer, H. E. Forcing native plants. Jour. Internat. Gard. Club. **2**: 119–123. Mr 1918. [Illust.]

Dunbar, J. Notes on Cotoneasters. Jour. Internat. Gard. Club **2**: 83–85. Mr 1918. [Illust.]

Fairchild, D. Gardens for plant breeders. Jour. Heredity **9**: 112–116. *f. 5–8.* Mr 1918.

Faulwetter, R. C. The *Alternaria* leaf-spot of cotton. Phytopathology **8**: 98–105. *f. 1–3.* Mr 1918.

Fink, B. The distribution of fungi in Porto Rico. Mycologia **10**: 58–61. Mr 1918.

Fitzpatrick, H. M. Sexuality in *Rhizina undulata* Fries. Bot. Gaz. **65**: 201–226. *pl. 3, 4.* 15 Mr 1918.

Frye, T. C. The rhacomitriums of western North America. Bryologist **20**: 91–98. *pl. 20–23.* 5 D 1917; **21**: 1–16. *pl. 1–14.* 15 Mr 1918.

Fuller, G. D., & Bakke, A. L. Raunkiaer's "life forms," "leaf-size classes," and statistical methods. Plant World **21**: 25–37. *f. 1.* F 1918.

Galloway, B. T. Some of the broader phytopathological problems in their relation to foreign seed and plant introduction. Phytopathology **8**: 87–97. Mr 1918.

Gruber, C. L. Herbs with fleshy fruits. Am. Bot. **24**: 13, 14. F 1918.

Hanson, H. C. The invasion of a Missouri river alluvial flood plain. Am. Mid. Nat. **5**: 196–201. *pl. 1, 2.* Mr 1918.

Harper, E. T. The *Clavaria fistulosa* group. Mycologia **10**: 53–57. *pl. 3–5.* Mr 1918.

Harper, E. T. Two remarkable Discomycetes. Bull. Torrey Club **45**: 77–86. *pl. 1–3.* 7 Mr 1918.
Underwoodia columnaris and ***Pustularia gigantea.***

Harper, R. M. Some dynamic studies of Long Island vegetation. Plant World **21**: 38–46. *f. 1, 2.* F 1918.

Harris, J. A., & Avery, B. T. Correlation of morphological variations in the seedling of *Phaseolus vulgaris.* Bull. Torrey Club **45**: 109–119. 1 Ap 1918.

Hendrickson, A. H. The common honey bee as an agent in prune pollination. Calif. Agr. Exp. Sta. Bull. 291: 215–236. *f. 1–13.* Ja 1918.

Herrington, A. Lilies. Jour. Internat. Gard. Club **2**: 5–29. Mr 1918. [Illust.]

Hoffer, G. N. An aecium on red clover, *Trifolium pratense* L. Proc. Indiana Acad. Sci. **1916**: 325, 326. 1917.

Hoffer, G. N., & Holbert, J. R. Results of corn disease investigations. Science II. **47**: 246, 247. 8 Mr 1918.

Holmes, E. M. Medicinal herbs: their cultivation and preparation in Great Britain. Jour. Internat. Gard. Club **2**: 35–82. Mr 1918. [Illust.]

Jackson, H. S. Apple diseases in Indiana, with spray schedule. Indiana Agr. Exp. Sta. Circ. 7: 1–23. *f. 1–14.* S 1917.

Jackson, T. F. The description and stratigraphic relationships of fossil plants from the lower Pennsylvania rocks of Indiana. Proc. Indiana Acad. Sci. **1916**: 405–428. *pl. 1–10* + *f. 1.* 1917.

Fourteen new species are described in *Lepidodendron* (1), *Trigonocarpum* (3), and *Cardiocarpon* (10).

Jackson, H. S., & Osner, G. A. Potato diseases in Indiana. Indiana Agr. Exp. Sta. Circ. 71: 1–16. *f. 1–5.* S 1917.

Jones, L. R. Disease resistance in cabbage. Proc. Nat. Acad. Sci. **4**: 42–46. *f. 1, 2.* 15 F 1918.

Kendall, J. N. Abscission of flowers and fruits in the Solonaceae, with special reference to *Nicotiana*. Univ. Calif. Publ. Bot. **5**: 347–428. *pl. 49–53* + *f. 1–10.* 6 Mr 1918.

Knowlton, C. H., & Deane, W. Reports on the flora of the Boston District,—XXVI. Rhodora **20**: 15–18. 25 Ja 1918;—XXVII. Rhodora **20**: 55–59. 2 Mr 1918.

Long, B. History of the American record of *Scirpus mucronatus*. Rhodora **20**: 41–48. 2 Mr 1918.

Ludwig, C. A., & Rees, C. C. The structure of the uredinium in *Pucciniastrum Agrimoniae*. Am. Jour. Bot. **5**: 55–60. *pl. 8.* 9 Mr 1918.

Lunell, J. The collecting, drying and mounting of plant specimens. Am. Mid. Nat. **5**: 191–195. Mr 1918.

Lyman, G. R. The need of organization of American botanists for more effective prosecution of war work. Science II. **37**: 279–285. 22 Mr 1918.

Macbride, J. F. New or otherwise interesting plants, mostly North American Liliaceae and Chenopodiaceae. Contr. Gray Herb. II. **53**: 1–22. 26 F 1918.

Includes *Cirsium praeteriens, Lycium Spencerae, Lomatium Nelsonianum, Lotus Spencerae, Atriplex spinifera,* and *Tricyrtis clinata,* spp. nov. and several new varieties and new combinations.

MacCaughey, V. The native bananas of the Hawaiian Islands. Plant World **21**: 1–12. Ja 1918.

McGee, J. M. The imbibitional swelling of marine algae. Plant World **21**: 13–15. Ja 1918.

McKay, M. B., & Pool, V. W. Field studies of *Cercospora beticola.* Phytopathology **8**: 119–136. *f. 1, 2.* Mr 1918.

McNair, J. B. Secretory canals of *Rhus diversiloba.* Bot. Gaz. **65**: 268–273. 15 Mr 1918.

Middlebrook, C. A. Odorous flowers of Texas. Am. Bot. **24**: 3–6. F 1918.

Moore, G. T. Algological notes.—II. Preliminary list of algae in Devils Lake, North Dakota. Ann. Missouri Bot. Gard. **4**: 293–303. N 1917.

Moore, W., & Williams, J. J. Studies in greenhouse fumigation with hydrocyanic acid: physiological effects on the plant. Jour. Agr. Research **11**: 319–338. *pl. 34 + f. 1–11.* 12 N 1917.

Mottier, D. M. Chondriosomes and the primordia of chloroplasts and leucoplasts. Ann. Bot. **32**: 91–114. *pl. 1.* Ja 1918.

Munn, M. T. Neck-rot disease of onions. New York Agr. Exp. Sta. Bull. 437: 365–455. *pl. 1–11.* Jl 1917.

Murphy, P. A. The morphology and cytology of the sexual organs of *Phytophthora erythroseptica* Pethyb. Ann. Bot. **32**: 115–153. *pl. 2, 3.* Ja 1918.

Murrill, W. A. The Agaricaceae of tropical North America.—VII. Mycologia **10**: 15–33. 14 F 1918.

Includes 18 new species in *Atylospora* (11), *Psathyrella* (5), *Psilocybe* (1), and *Campanularius* (1).

Murrill, W. A. The Agaricaceae of tropical North America—VIII. Mycologia **10**: 62–85. Mr 1918.

Includes 29 new species in *Drosophila* (8), *Hypholoma* (1), *Gomphidius* (1), *Stropharia* (2), *Agaricus* (13), and *Coprinus* (4).

Murrill, W. A. Murrill's and Saccardo's names of polypores compared. 1–13. New York. 1918.

Nelson, J. C. Additions to the flora of western Oregon. Torreya **18**: 21–35. 8 Mr 1918.

Osner, G. A. Additions to the list of plant diseases of economic importance in Indiana. Proc. Indiana Acad. Sci. **1916**: 327–332. 1917.

Pammel, L. H., & Dox, A. W. The protein contents and microchemical tests of the seeds of some common Iowa weeds. Proc. Iowa Acad. Sci. **24**: 527–532. 1917.

Pipal, F. J. Weed seeds in the soil. Proc. Indiana Acad. Sci. **1916**: 368–377. 1917.

Popenoe, W. Avocados as food in Guatemala. Jour. Heredity **9**: 99–107. *f. 1–4.* Mr 1918.

Porter, A. A., & Coons, G. W. Differences between the species of *Tilletia* on wheat. Phytopathology **8**: 106–113. *f. 1–4.* Mr 1918.

Rathbun, R. The Columbian Institute for the promotion of arts and sciences. U. S. Nat. Mus. Bull. 101: 1–85. 18 O 1917.
Contains chapters on Botanical Gardens; Washington Botanical Society, etc.

Rice, T. B. A study of the relations between plant growth and combined nitrogen in Winona Lake. Proc. Indiana Acad. Sci. **1916**: 333–362. *f. 1–16.* 1917.

Rock, J. F. *Pelea* and *Platydesma*. Bot. Gaz. **65**: 261–267. *f. 1.* 15 Mr 1918.
Includes *Pelea Gayana* and *P. recurvata*, spp. nov.

Rosendahl, C. O. Observations on *Betula* in Minnesota with special reference to some natural hybrids. Minnesota Bot. Stud. **4**: 443–459. *pl. 49* + *f. 1, 2.* 20 S 1916.

Rosendahl, C. O., Observations on the morphology of the underground stems of *Symplocarpus* and *Lysichiton*, together with some notes on geographical distribution and relationship. Minnesota Bot. Stud. **4**: 137–152. *pl. 21, 22* + *f. 1, 2.* 15 S 1911.

Rosendahl, C. O., & Butters, F. K Reputed Minnesota plants which probably do not occur in the state. Minnesota Bot. Studies **4**: 461–473. 20 S 1916.

Sax, H. J. Spore formation in *Philocopra coeruleotecta*. Am. Jour. Bot. **5**: 61–78. *pl. 9–11.* 9 Mr 1918.

Schaffner, J. H. The expression of sexual dimorphism in heterosporous sporophytes. Ohio Jour. Sci. **18**: 101–125. *f. 1–28.* F 1918.

NISHIMURA: CARRIER OF THE MOSAIC DISEASE